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Reithrodontomys raviventris. By Howard Shellhammer

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Reithrodontomys raviventris Dixon, 1908 Salt Marsh Harvest Mouse

Reithrodontomys raviventris Dixon, 1908:197. Type locality salt marsh near Redwood City, San Mateo County, California. Reithrodontomys halicoetes Dixon, 1909:271. Type locality 3 mi S Petaluma, Sonoma County, California.

CONTEXT AND CONTENT. Order Rodentia, Family Cricetidae, Subfamily Cricetinae, Subgenus *Reithrodontomys*. Two subspecies of *Reithrodontomys raviventris* are recognized (Howell, 1914).

R. r. raviventris Dixon, 1908:197, see above. R. r. halicoetes Dixon, 1909:271, see above.

DIAGNOSIS. Externally Reithrodontomys raviventris is similar in appearance to R. megalotis longicaudus in the San Francisco Bay region (Fig. 1). The length of the tail is longest in Suisun Bay populations and shortest in Santa Clara County populations and tail/body ratios are useful in diagnosis in these two areas. The thickness of the tail at 20 mm from the body is the most useful feature in identification as R. raviventris has a thicker tail (2.1 to 3.0 mm) than R. megalotis (generally 1.9 to 2.0 mm). The tip of the tail is blunt and the tail is unicolored or nearly so. No white hairs are found on the underside of the tail in typical salt marsh harvest mice, although considerable variation exists. The pelage is usually darker and the venters of individuals of R. r. raviventris (the southern subspecies) are usually cinnamon-colored. There is, however, clinal variation in the color of the venter. Most individuals of R. r. halicoetes and northern populations of R. r. raviventris have white venters, even whiter than those of R. megalotis. For a complete discussion of the morphological differences between these mice see Fisler (1965).

Only two characteristics of the cranium (Fig. 2) are known to be diagnostic. Reithrodontomys raviventris has a significantly longer length of braincase (Fisler, 1965) and a relatively and significantly shorter distance between the anterior end of the posterior palatine foramen and the posterior end of the incisive foramen as compared to the length of the palate from the latter point to its posterior end (Shellhammer, in press). The phallus, the simple, slightly-curved baculum, and the vagina of R. raviventris are significantly shorter than those of R. megalotis (Fisler, 1965). The baculum does not exhibit diagnostic morphological differences.

GENERAL CHARACTERS. Some ranges of measurements (in mm) from Fisler (1965) are: total length, 118 to 175; length of tail, 56 to 95; hindfoot, 15 to 21; length of skull, 19.5 to 22.4; depth of braincase, 6.1 to 7.6; width of intermeatus, 6.7 to 8.5; breadth of braincase, 9.2 to 11.0; length of rostrum, 8.9 to 10.9; length of braincase, 9.5 to 10.9; length of nasals, 6.5 to 8.5; length of incisive foramen, 3.7 to 4.5; and weight, 7.6 to 14.5 g.

The upper parts of R. r. raviventris are blackish and cinnamon. A lateral line is present as a tawny stripe. The venter varies from white to cinnamon (see Fisler, 1965, for a complete description). The upperparts of R. r. halicoetes are lighter than in R. r. raviventris but darker than in R. megalotis. A lateral line is seldom present and the venter is usually white. The ears of both subspecies are dark; those of R. r. raviventris blackish. Most salt marsh harvest mice have tufts of ochraceous hairs at the anterior bases of their ears. The pelage of salt marsh harvest mice is longer and thicker than R. megalotis at all seasons.

The tails of salt marsh harvest mice are indistinctly bicolored. There are always brownish hairs on the under surface, something absent from the bicolored tail of *R. megalotis*.

DISTRIBUTION. Reithrodontomys raviventris is restricted to the salt and brackish water marshes adjoining San Francisco Bay and its tributaries. The northern subspecies, R. r. halicoetes, is found from the Gallinas Creek area on the Marin Peninsula

through the Petaluma, Napa and Suisun Bay marshes, and across the Carquinez Straits to the northern Contra Costa County coast (Fig. 3). The eastern extent of the range of this subspecies on the north side of the Straits is approximately 5 km E Collinsville, Solano County. The range of the Contra Costa population extends from Martinez on the west to the Antioch area on the east. The extension of the range of this species to Knights Landing, Yolo County, by Howell (1914) and shown in Hall and Kelson (1959) is discounted.

The southern subspecies, R. r. raviventris, has a disjunct distribution, with a small population at Corte Madera, Marin County, quite near the Gallinas populations of R. r. halicoetes. Additionally, there is a population near Point San Pedro in northwestern Contra Costa County. The populations noted by Fisler (1965), near San Leandro, Alameda County, have disappeared, hence this subspecies is mostly restricted to a band extending from Belmont, San Mateo County, on the San Francisco Peninsula to the Newark area in Alameda County. The largest area of appropriate marsh in this band is near its eastern end in the Newark area.

The tidal marshes of the San Francisco Bay system have been greatly reduced (most estimates are by 79% or more) by filling, diking, and land subsidence followed by flooding. Most of the marshes, therefore, have become long, narrow areas along outboard dikes. The only major exceptions to this pattern are the Petaluma Marsh, the north-central San Pablo Bay marshes (which are growing larger), several marshes on the Contra Costa Coast and some of the marshes in the Newark area. The Suisun Bay marsh has been managed for waterfowl and although the marsh areas are large, most are diked and managed for alkali bullrush, Scirpus robustus, a habitat little used by salt marsh harvest mice.

There are no known fossils of R. raviventris.

FORM AND FUNCTION. No anatomical studies have been reported for *R. raviventris* other than that of Fisler (1965), who studied fourteen cranial, body, and pelage characters.

Fisler (1965) demonstrated that both subspecies, which probably consume considerable amounts of green vegetation, have longer intestines than their progenitor species, *R. megalotis*, which is primarily a seedeater.

Fisler (1963, 1965) demonstrated that R. r. raviventris is unable to drink sea water, selecting water with salinities between fresh and sea water but closer to the latter. R. r. halicoetes, on the other hand, can drink sea water (Fisler, 1963; Haines, 1964). Fisler (1965) noted that R. r. halicoetes lives in marshes where the range of salinities is great but where the average salinity (<22 per thousand) is not great. The southern subspecies, however, lives in marshes where the salinity is high and relatively stable (27.0 to 31.2 per thousand) throughout the year.

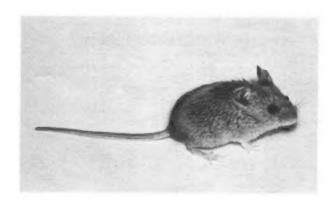
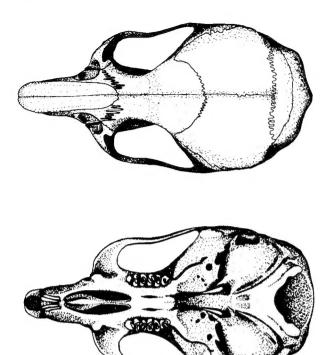


FIGURE 1. Adult Reithrodontomys raviventris.

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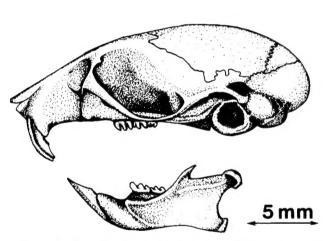


FIGURE 2. Dorsal, ventral and lateral views of the cranium and lateral view of mandible of *Reithrodontomys raviventris*.

Fisler (1965) noted that R. r. raviventris has the ability to become torpid in early morning and that this ability varies individually. Shellhammer (unpubl. observ.) found individuals so torpid that 0.5 h of exposure to human body warmth was necessary for them to become active again. R. r. halicoetes apparently does not become torpid.

ONTOGENY AND REPRODUCTION. Fisler (1965) believed that R. r. halicoetes males were probably not very active reproductively in December and January, and males of R. r. raviventris were probably inactive from November (possibly October) through January. Males of R. r. raviventris are sexually active from April through September, whereas most breeding by females was from March through November (Fisler, 1965). The breeding season for R. r. halicoetes was shorter, apparently May through November; hence, individuals of this subspecies may only produce one litter per year.

Fisler (1965) noted that R. r. halicoetes had an average litter size of 3.7 to 3.9; R. r. raviventris had an average of 4.0 although the latter figure was based on a sample size of only 14 litters.

ECOLOGY. Reithrodontomys raviventris is dependent on plant cover; it moves into grasslands bordering marshes only in spring and summer when grasslands provide maximum cover

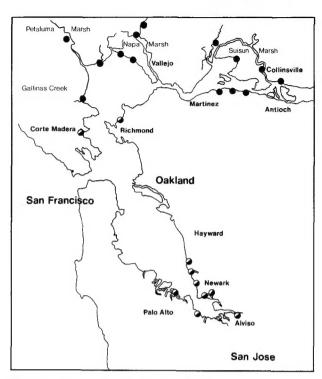


FIGURE 3. Geographic distribution of Reithrodontomys raviventris in the San Francisco Bay Region of California. Only principal populations are noted. Dark circles indicate R. raviventris halicoetes and half-dark circles indicate R. r. raviventris.

(Fisler, 1965; see also Zetterquist, 1978). Fisler (1965, 1968) detailed movements of salt marsh harvest mice within marshes as well as the use of marshes by *R. megalotis*. Shellhammer (1977) studied intermarsh movements in the Alviso area, Santa Clara County, and found no movements between marshes separated by a dike road as little as 3 m wide.

Fisler (1965) noted that the mid-marsh areas of many marshes throughout the San Francisco Bay region were increasing in the amount of Salicornia spp., especially Salicornia pacifica. Shellhammer (1977) and Wondolleck et al. (1976) noted that areas of S. pacifica were preferred as habitat, especially when the upper marsh and transition areas were removed by filling or diking. Both authors also noted that low-marsh areas, especially those dominated by Spartina foliosa, were not used by salt marsh harvest mice. Shellhammer (in press) noted that solid stands of Scirpus robustus are little used even though this plant is a mid-marsh species.

Shellhammer (1977) enumerated the major threats to the habitat of salt marsh harvest mice which include filling, diking, subsidence, and changes in salinity. A few marshes, such as the one on the northern edge of San Pablo Bay, are growing because of increased sedimentation at their bayward edges. Most marshes studied by Fisler in the late 1950's and early 1960's have been reduced in size or quality since then, or have been destroyed. Loss of habitat has been greatest in the range of R. r. raviventris. Wondolleck et al. (1976) studied the Palo Alto salt marsh and noted that the Spartina-dominated portions of the marsh had increased from the 10% of the marsh noted by Hinde (1954) to 70%. Concurrently the Salicornia areas decreased from 90% to less than 10% and the mice were concentrated in the Salicornia areas. The Palo Alto-Alviso area has undergone considerable subsidence which has induced the changes in vegetation at Palo Alto and throughout the Alviso marshes (Shellhammer, 1977). Decreased salinities in the Alviso area of southern San Francisco Bay, due to increasing volumes of non-saline, treated sewage water, is changing major Salicornia marshes to nearly uniform Scirpus robustus marshes (Shellhammer, 1977).

Decreased flow of fresh water through the Sacramento River system (Mall, 1969) is causing floristic changes in Suisun Bay marshes; in particular, there has been an increase in Salicornia. Many areas formerly dominated by brackish-water species typified by Typha, Scirpus, and Juncus spp. are now dominated by salt-loving species of Salicornia, Atriplex, and Distichlis.

Diking and filling have destroyed most transition areas, es-

pecially in the southern San Francisco Bay. Introduced Atriplex semibacatta borders the dikes and is heavily used as an upland refugium during certain times of the year and various phases of tidal cycles (Rice, 1974; Shellhammer, unpubl. observ.; Zetterquist, 1978). In many subsided areas of the southern San Francisco Bay, usable portions of former marshes have been reduced to narrow strips along dikes (Rice, 1974).

Marginal areas used by R. r. raviventris are usually hypersaline diked areas with reduced plant diversity and cover. Zetterquist (1978) found salt marsh harvest mice in a number of such areas and found that animals were most likely to be trapped in the most saline areas. Shellhammer (in Biosystems Analysis, 1979; Envirodyne Engineers, 1978) studied R. r. halicoetes in similar but less saline conditions in the northeastern portion of the range of the species at Collinsville, Solano County, and found moderate populations using predominantly Salicornia areas.

BEHAVIOR. Fisler (1965) and Shellhammer (1977) noted the relative calmness of *R. raviventris* as compared to the nervousness or tenseness of *R. megalotis*. The latter species acts like *Mus musculus* in that it is very active, bites a lot, and jumps from traps without hesitation. Salt marsh harvest mice tend to be placid, bite relatively little, remain balled up in the cotton of traps, and are more deliberate to their movements. So typical are the behaviors of the two species that Shellhammer (in press) used behavior as a secondary diagnostic feature in the field. These differences in behavior have been associated with the habitat preferences of the two species by Fisler (1965). Salt marsh harvest mice are highly dependent on cover which varies seasonally.

Neither subspecies burrows (Fisler, 1965). Individuals of R. r. halicoetes build ball-like nests quite like those of R. megalotis. These balls of dry grasses and/or sedges are usually placed on the ground surface and probably are rebuilt quickly when wetted by the waters of high tides (Fisler, 1965). R. r. raviventris apparently does little nest building. Shellhammer (unpubl. observ.) noted loosely organized nests of dry grasses built on the ground surface, whereas Fisler (1965) saw no mouse nests that he could associate with certainty with R. r. raviventris. Johnston (1956) reported that these mice roofed over at least five old nests of song sparrows.

Fisler (1965) reported that individuals of both subspecies swim calmly and well. They are buoyant and their fur does not wet nearly as quickly as that of R. megalotis.

GENETICS. Individuals of both subspecies have 2n = 38 chromosomes but there are some differences in the structure of their chromosomes (Shellhammer, 1967). R. r. halicoetes has 14 metacentric, 16 submetacentric and 6 subtelocentric autosomes, and R. r. raviventris has 10 metacentric, 18 submetacentric and 8 subtelocentric autosomes. All of the moderate sample (n = 27) of R. megalotis in that study had 2n = 44, but later studies (Blanks and Shellhammer, 1967; Shellhammer, 1969) found a basic diploid number of 42, with from 1 to 7 additional supernumerary chromosomes for R. megalotis. Shellhammer (1969) hypothesized that the 2n = 42 condition of R. megalotis was primitive and that the 2n = 38 of R. raviventris was derived.

REMARKS. Reithrodontomys raviventris was declared an Endangered Species by the United States Department of the Interior in 1970 and the California Department of Fish and Game in 1971. The northern subspecies, R. r. halicoetes, occupies the largest and least modified areas of marsh, located furthest away from large urban areas. Field studies were carried out in 1980 to assess the population status of the two subspecies (Gilroy and Shellhammer, 1980; Harvey and Stanley Associates, 1980; Simons and Shellhammer, 1981).

LITERATURE CITED

Biosystems Analysis, Inc. 1979. Technical report of the 1979 summer trapping program for the endangered salt marsh harvest mouse at the Montezuma Power Plant Site. Prepared for Pacific Gas and Electric Company, Dept. Engin. Res., San Ramon, California, 16 pp. Blanks, G. A., and H. S. Shellhammer. 1968. Chromosome polymorphism in California populations of harvest mice. J. Mamm., 49:726-731.

- Dixon, J. 1908. A new harvest mouse from the salt marshes of San Francisco Bay, California. Proc. Biol. Soc. Washington, 21:197-198.
- 1909. A new harvest mouse from Petaluma, California. Univ. California Publ. Zool., 5:271–273.
- Envirodyne Engineers. 1978. Salt marsh harvest mouse trapping and vegetation survey at the Montezuma Power Plant Site, Fossil Fuel 1 & 2 Project. Prepared for Pacific Gas and Electric, Dept. Engin. Res., San Ramon, California, 53 pp.
- Fisler, G. F. 1963. Effects of salt water on food and water consumption and weight of harvest mice. Ecology, 44:604-608.
- 1965. Adaptations and speciation in harvest mice of the marshes of San Francisco Bay. Univ. California Publ. Zool., 77:1-108.
- 1968. Adaptations in movement patterns of two species of salt marsh rodents. Bull. So. California Acad. Sci., 67:96-103.
- Gilroy, A., and H. Shellhammer. 1980. Trapping survey of salt marsh harvest mice, Reithrodontomys raviventris raviventris, in the marshes of South San Francisco Bay during the summer of 1980. Report to the San Francisco Bay Natl. Wildl. Refuge, Newark, 27 pp. (revised, 1981).
- Haines, H. 1964. Salt tolerance and water requirements in the salt-marsh harvest mouse. Physiol. Zool., 37:266-272.
- Hall, E. R., and K. R. Kelson. 1959. The mammals of North America. The Ronald Press Company, New York, 2:547– 1083 + 79.
- Harvey and Stanley Assoc. 1980. Status of the salt marsh harvest mouse (*Reithrodontomys raviventris*) in Suisun Marsh. Prepared for Water and Power Res. Ser., Sacramento, California, 52 pp.
- Hinde, H. P. 1954. Vertical distribution and salt marsh phanerograms in relation to tide levels. Ecol. Monog., 24:209-225.
- Howell, A. H. 1914. Revision of the American harvest mice. N. Amer. Fauna, 36:1-97, plates 1-7.
- Johnston, R. F. 1956. Predation by short-eared owls in a Salicornia salt marsh. Wilson Bull., 68:91-102.
- Mall, R. E. 1969. Soil-water-salt relationships of waterfowl food plants in the Suisun Marsh of California. Wildl. Bull., California Dept. Fish and Game, 1:1-59.
- Rice, V. 1974. The population ecology of the salt marsh harvest mice at triangular marshes. Unpubl. M.A. thesis, San Jose State Univ., San Jose, California, 127 pp.
- Shellhammer, H. 1967. Cytotaxonomic studies of the harvest mice of the San Francisco Bay region. J. Mamm., 48:549-556.
- 1969. Supernumerary chromosomes of the harvest mouse, Reithrodontomys megalotis. Chromosoma (Berlin), 27:102-108.
- 1977. Of mice and marshes. San Jose Studies, San Jose State Univ., 3(1):23-35.
- In press. Identification of salt marsh harvest mice, Reithrodontomys raviventris, in the field and with cranial characteristics. California Fish and Game.
- Simons, L., and H. Shellhammer. 1981. Trapping survey of salt marsh harvest mice *Reithrodontomys raviventris hali*coetes) during the summer of 1980. California Fish and Game, Nongame Wildl. Invest. Final Rep., E-W-4, V-3.1.
- Wondolleck, J., W. Zolan, and L. Stevens. 1976. A population study of harvest mice in the Palo Alto Salt Marsh. Wasmann J. Biol., 34:52-64.
- Zetterquist, D. 1978. The salt marsh harvest mouse (Reithrodontomys raviventris raviventris) in marginal habitats. Wasmann J. Biol., 35:68-76.

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